NOTES ON THE FIRST CLEAVAGE OF LEPAS.

MAURICE A. BIGELOW.

ALL previous observers of the development of the Cirripede ova have agreed that the polar bodies are formed at the protoplasmic end of the ellipsoidal ovum. The first cleavage plane has usually been described as almost transverse to the long axis of the ovum. Ova in which the first cleavage plane was oblique and sometimes almost parallel to the long axis have been described as occasionally occurring. These have been regarded as variations from the normal cleavage. The conclusion has seemed unavoidable that the first cleavage plane is equatorial, and that it does not pass through the animal pole, as is the case in nearly all ova. Such are the conclusions of Groom ('94),[1] the latest investigator of the development of Cirripedia. The writer ('96)[2] found that in *Lepas fascicularis* the second polar body lies in the first cleavage furrow, the first one being outside the vitelline membrane. This position of the second polar body indicated that the first cleavage furrow passed through the animal pole of the ovum, but no observations were made which explained this position of the polar body apparently 90° removed from the point of its formation. Nussbaum ('87)[3] found similar relations existing in the ovum of *Pollicipes*, and assumed that the first cleavage furrow forms in the long axis of the ovum passing through the animal pole, and that it later rotates to the transverse position. The evidence which he offered in favor of his assumption was apparently shown to be incorrect by the subsequent observations of Groom.

In the course of comparative studies of the early develop-

[1] Groom, T. T. ('94), "Early Development of Cirripedia," *Phil. Trans.* Vol. clxxxv B, pp. 119–232.

[2] Bigelow, M. A. ('96), "Early Development of Lepas fascicularis," a preliminary note, *Anat. Anz.* Vol. xii, pp. 263–269.

[3] Nussbaum, M. ('87), "Vorläufiger Bericht," *Sitz. Berlin Akad.* 1887. pp. 1051–55. — ('90), "Anatomische Studien an Californischen Cirripedien." Bonn.

ment of several Cirripedia from the standpoint of cytogeny, the writer has recently been able to make observations on the living ova of *L. anatifera*, which explain the various conflicting observations and determine the relations of the first cleavage plane. Some mechanical effects have also been observed, which seem to contribute something of interest to the study of the mechanics of development. Some notes on the observations are given here; a detailed account with discussion is reserved for a future paper.

A brief description of the unsegmented ovum will serve as a basis for the discussion of the cleavage. The ovum of *L. ana-*

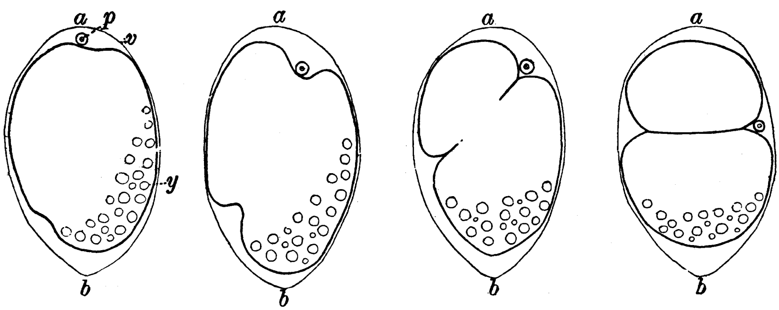

FIG. 1. FIG. 2. FIG. 3. FIG. 4.

Camera drawings of the living ovum, showing the rotation of plane of cleavage. *a–b* marks the constant long axis of the vitelline membrane (*v.*), *p* indicates the second polar body, and *y* the yolk spherules.

tifera just before the beginning of cleavage is ellipsoidal in form. The yolk spherules at this time lie aggregated at one pole, which is known to be the ultimate posterior; but during the preparation for division the yolk shifts to one side of the polar area (Fig. 1). The vitelline membrane closely surrounding the ovum is rounded at the anterior and somewhat pointed at the posterior pole. It is apparently quite rigid and does not greatly alter in shape during the embryological development. The second polar body lies within the vitelline membrane at the anterior end of the ovum (Fig. 1).

Figs. 1–4 illustrate the changes in the external form of the ovum during the first cleavage. They are from camera lucida drawings of a living ovum, made at intervals of four minutes. They were selected from a series of fourteen drawings

made at intervals of one minute. The vitelline membrane occupied a fixed position with reference to lines on the slide and on the drawing board. The line *a–b* marks the long axis of the vitelline membrane, which before cleavage passed through the animal pole of the ovum. The cleavage furrow appeared in a plane passing through the animal pole and oblique to the long axis of the ovum (Fig. 1). As the cleavage furrow slowly deepened, the plane of cleavage rotated until, at the time of complete separation of the first two blastomeres, it was almost always transverse to the original long axis of the ovum; that is, it occupied a position at right angles to its first position, which was still clearly indicated by the unaltered form of the vitelline membrane (*a–b*, Fig. 4). In some ova observed the rotation was less, and at the close of the cleavage the plane of separation was oblique to the original long axis of the ovum. Such a condition would be well represented by Fig. 3, if the separation of the blastomeres were there shown as complete.

Along with this rotation of the cleavage plane there occurred a shifting of the position of the second polar body, which was in the cleavage furrow, and was followed to a position about 90° from the point of its formation (Figs. 1–4). Occasionally the polar body became detached from the ovum and failed to shift with the rotating furrow. This seems to explain the few cases observed by Groom, upon which he based his view that the first cleavage is usually formed transversely to the long axis of the ovum, and does not pass through the animal pole. Studies of the preserved material of several other species and genera lead me to believe that such a rotation takes place also in them. The polar bodies are formed in a position about 90° from that finally occupied by the first cleavage plane. There is reason for believing that this plane passes through the animal pole, for the second polar body is found in the cleavage furrow. The relations to the vitelline membrane are as in *L. anatifera*. These considerations make it very probable that in the case of all *Lepadidae* and *Balanidae*, whose development has been heretofore described, a rotation of the cleavage plane will be found to account for the apparently equatorial position of the first plane of cleavage.

A study of sections of the ova at various stages in the first cleavage shows that the mitotic spindle is at first oblique to the long axis of the ovum and nearly perpendicular to the plane in which the furrow first appears (Fig. 5). As cleavage progresses, the spindle turns with the plane of cleavage and at last comes to lie in the long axis of the partially divided ovum (Figs. 6 and 7). The amount of its rotation is approximately

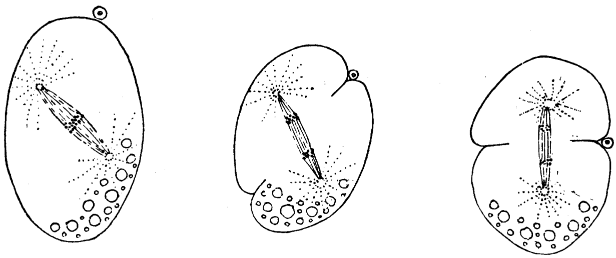

FIG. 5. FIG. 6. FIG. 7.

Drawings of sections of ova in stages of cleavage corresponding approximately with those shown in Figs. 1, 2, and 4, respectively.

equal to that of the cleavage plane. From what follows it will appear that the rotation of the spindle is produced by the movement of the dividing cell-body.

The rotation of the first cleavage plane appears to be secondary to the cleavage processes and capable of an explanation along mechanical lines. The cleavage furrow appears in an almost longitudinal position, passing through the animal pole. As the furrow deepens, the forming cells tend to become spherical and hence lengthen the axis of the ovum perpendicular to the plane of cleavage. If no firm envelope confined the ovum and interfered with change in its form, the long axis of the two-cell stage would lie perpendicular to the plane in which cleavage begins; but the vitelline membrane evidently interferes with extension in this direction. As the cleavage progresses, therefore, and the resulting cells become more and more spherical (Figs. 2–3), a rotation of the ovum becomes necessary, for evidently the long axis of the two-cell stage must approximately coincide with that axis of the vitelline membrane. An examination of the figures makes it appear that, as the forming blastomeres become more spherical and consequently lengthen the

axis of the ovum perpendicular to the plane of cleavage, pressure is obliquely applied to the vitelline membrane with the result that the ovum as a whole rotates, and gradually the dividing ovum adjusts itself to the form of the vitelline membrane. The cleavage plane becomes transverse or oblique, depending upon the amount of rotation necessary to meet adjustment. With a relatively wide vitelline membrane the rotation is less than 90°, for the divided ovum can then become adjusted to an oblique axis of the membrane, and the cleavage plane consequently remains oblique.

The observations recorded above have been repeated on many ova from different individuals, so there can be no doubt that a normal condition is described.

MARINE BIOLOGICAL LABORATORY,
WOODS HOLL, MASS.,
August 30, 1898.